SANDAKANIA 6 (1995): 15–39

Pollination in the rattans *Calamus subinermis* and *C. caesius* (*Palmae : Calamoideae*)

Y.F. Lee[1], K. Jong[2], M.D. Swaine[2], V.K. Chey[1] & A.Y.C. Chung[1]

[1]Forest Research Centre,
P.O. Box 1407, 90008 Sandakan,
Sabah, Malaysia

[2]Department of Plant & Soil Science, University of Aberdeen,
Cruickshank Building, St. Machar Drive, Aberdeen AB9 2UD,
Scotland, United Kingdom

Summary. Observations on the visitors to four inflorescences of *Calamus subinermis* H. Wendl. *ex* Becc. and seven inflorescences of *C. caesius* Bl. in research plots located in the Sandakan Residency, and examination of the pollen loads on the visitors, show that the principal pollinators in these two species of rattan are pyralid, noctuid and other moths which are active at night. The diurnally active trigonids and other Hymenoptera, as well as other insect visitors, are not thought to play a significant role because pollen release is mostly nocturnal. Pollen dispersed by wind and collected with sticky suspended slides shows that wind may contribute to some short-distance pollination. The high pollen : ovule ratio estimated in this study confirms that the two dioecious species are out-crossing. The limited foraging ranges of the small moths may result in restricted gene exchange between populations, which may be adequate to allow allopatric speciation and may partly account for the high intra-generic diversity in *Calamus*.

Calamus subinermis H. Wendl. *ex* Becc. and *C. caesius* Bl. are respectively the commercially most important large-diameter and small-diameter native rattans in Sabah. Owing to inadequate control on exploitation, many populations of these species are endangered or extinct. For example, on the Sandakan Peninsula, the natural population

of *C. subinermis* is extinct; the nearest extant natural population is located on Berhala Island about 1.5 km from the peninsula, in *kerangas* (heath) forest—a forest type which is also abundant on the peninsula. In an effort to conserve representative samples of the extant populations for future breeding programmes, *ex situ* populations of these two and other species have been established by the state-owned Innoprise Corporation Sdn. Bhd. (Garcia *et al.* 1993) and those of *C. subinermis* by the Sabah Forestry Department. Pollination was investigated as part of a programme to gain an understanding of the genetic diversity of the two commercially important species. Pollination mechanism largely determines the extent of gene flow in these and other rattan species, although dispersal of seeds, which is usually by gravity and occasionally by birds and other animals, and other propagules, also influences the pattern of genetic diversity observed in nature.

Previous research on pollination in *Calamus* and related genera

Reports on the pollination of this dioecious genus and other rattans have hitherto been based on static observations on the inflorescences during daylight hours and inferences from the structure of the inflorescences. Beccari (1911) reported the presence of nectaries in two species of *Daemonorops*, a genus closely related to *Calamus*. Corner (1966) postulated that hapaxanthic rattans (e.g., *Korthalsia*, *Plectocomia* and *Plectocomiopis*) are melittophilous. Dransfield (1979) reported trigonids and honey bees visiting male flowers of *Plectocomia* sp. Insect pollination was also suggested by Madulid (1980) in *Plectocomia*, which has extremely fragrant flowers and conspicuous inflorescences visited by insects at anthesis. In most species of *Daemonorops*, *Ceratolobus*, *Calospatha* and *Calamus* section *Platyspathus*, the inflorescences are wholly or partially enclosed by bracts at anthesis, emit a musty odour and are visited by many beetles which were suggested by Dransfield (1979) to be pollinators. In other sections of *Calamus*, the inflorescences are lax and are not enclosed by bracts, and have been reported by Dransfield (1979) to produce a sour odour and to be visited mostly by wasps or flies. Kiew and Muid (1989) reported visits of *Trigona melina* to the male, but not the female, flowers of *Daemonorops didymophylla*. Uhl and Dransfield (1987) also suggested bees to be the most likely pollinators of many species of *Calamus*, although in some instances they may in fact be pollen thieves.

The present study was undertaken to shed more light on the pollination biology of the *Calamus* species.

Materials and methods

Phenological observation was carried out at fortnightly intervals in the *Calamus subinermis* plots in the Sepilok Arboretum (longitude 117°58'E, latitude 5°49'N) and

Berhala Island (longitude 118°10'E, latitude 5°51'N), and *C. caesius* plots in Kolapis A (longitude 117°35'E, latitude 5°47'N) and the Sepilok Arboretum. All of these plots are located in the Sandakan Residency in Sabah. The work on pollination was carried out during the flowering season.

Insect Pollination

During anthesis (defined here as the opening of the male flowers followed by the release of pollen from the anthers, and the emergence and development of the stigmas of the female flowers before they shrivel) of the accessible inflorescences, the visitors to as many stems as were feasible to sample were recorded for as long a duration as possible. Table 1 shows the inflorescences to which the visitors were observed and the duration of the observations. In the earlier observations prior to September, 1993 (i.e., observations 1.1, 1.2, 2.1–2.3, 2.6 and 2.7), the species of the visitors were identified and their abundance was recorded qualitatively. Observations carried out during and after September, 1993 (i.e., observations 1.3, 1.4, 2.4 and 2.5), included quantitative assessment of the abundance by counting all the visitors. All unknown visitors were captured for identification, and vouchers of all species were kept. It has been observed that the male flowers of both species usually open at dusk and shrivel and fall off from midnight onwards, and the fallen flowers still contain about 20% of the pollen present prior to anthesis (see Results). Pollen viability has also been noted to be significant (>10%) 2 days after anthesis (Lee, unpublished data). Therefore, visitors to fallen flowers were also recorded.

Representative samples of the common visitors to both female and male flowers of both rattan species were captured and examined under a microscope at X50 and X100 magnification to estimate the comparative pollen load. The number of pollen grains per mm^2 of the part of the body bearing pollen was estimated.

Wind Pollination

The possibility of wind pollination in *C. subinermis* was investigated in two isolated flowering male stems in Berhala Island in September, 1993, and January, 1994. Greased slides were suspended horizontally at a range of distance (0–20m) from the male inflorescences undergoing anthesis, at the same level as the inflorescences, for 24 hours. In September, 1993, petroleum jelly (Vaseline) and grease (Shell automotive multipurpose grease) were used, and it was found that grease gave better results as it resulted in less diffraction of light when the slides were examined under the microscope. In January, 1994, only grease was used. The slides were then brought back to the

Table 1. Inflorescences to which visitors were observed in the study on pollination of *Calamus subinermis* and *C. caesius*.

Species	Observation no.	Sex of inflorescence observed	Date of observation	Time of observation	Location of inflorescence	Clump and stem number	Quantitative (Qt) or Qualitative (Ql) record of visitors
Calamus subinermis	1.1	Female	29 Apr–11 May 91	06.00–16.00	Sepilok Arboretum	21.1	Ql
	1.2	Female	12 May–14 May 93	16.00–07.00	Sepilok Arboretum	21.2	Ql
	1.3	Male	07 Sep–09 Sep 93	12 noon–12 noon	Berhala Island	02.1	Qt
	1.4	Female	28 Sep–29 Sep 93	10.30–10.30	Berhala Island	48.1	Qt
Calamus caesius	2.1	Male	23 Sep–27 Sep 91	06.30–16.30	Sepilok Arboretum	20.2	Ql
	2.2	Male	23 Sep–27 Sep 91	06.30–16.30	Sepilok Arboretum	21.48	Ql
	2.3	Male	23 Oct–25 Oct 91	08.30–12.30	Kolapis A	–	Ql
	2.4	Male	20 Sep 93	17.30–midnight	Sepilok Arboretum	–	Qt
	2.5	Female	29 Sep 93	17.30–23.00	Sepilok Arboretum	–	Qt
	2.6	Female	04 Oct 93	08.45–11.30	Sepilok Arboretum	–	Ql
	2.7	Male	04 Oct 93	08.45–11.30	Sepilok Arboretum	–	Ql

laboratory and examined under a microscope at ×100 magnification. For each slide the pollen grains observed in 10 randomly chosen views of 5.31 mm^2 were counted and the density of pollen grains on each slide was estimated. For *C. caesius*, pollen dispersal by wind was not investigated because it was not possible to locate an accessible isolated inflorescence to set up the sticky traps along unobstructed paths.

Estimation of pollen grains in flowers and pollen : ovule ratio

Preliminary observations have shown that the male flowers shrivel and fall off a few hours after anthesis, but a substantial proportion (>10%) of the pollen is still viable 2 days after anthesis. Moreover, insect visitors have been observed on fallen male flowers (see Results). To get a clearer picture of the destiny of the pollen, the pollen grains in the intact and fallen male flowers were estimated. Staminate flower buds and fallen flowers were collected from an inflorescence each of two stems of *C. subinermis* on Berhala Island and two stems of *C. caesius* in the Sepilok Arboretum. The anthers of a flower or a flower bud were dissected out and crushed in a petri dish containing water and a drop of detergent, and any remaining pollen grains on the flower were washed into the dish. The resulting suspension was stirred thoroughly before the pollen grains were counted under a light microscope at ×100 magnification to estimate the number of pollen grains. Altogether 5 intact flower buds and 5 fallen flowers from each inflorescence were examined.

To confirm the obligate xenogamy (cross fertilization) in these two dioecious species, the pollen : ovule ratio in the population of *C. subinermis* on Berhala Island was estimated by recording:

(i) (a) number of female stems (N)
    (b) number of male stems (n)
(ii) (a) average number of inflorescences produced per female stem (I)
    (b) average number of inflorescences produced per male stem (i)
(iii) (a) average number of flowers per female inflorescence (F)
    (b) average number of flowers per male inflorescence (f)
(iv) (a) estimated number of pollen grains per male flower (P)
    (b) estimated number of ovules per female flower (O)

Pollen : ovule ratio was then calculated as $(P \times f \times i \times n) / (O \times F \times I \times N)$.

The pollen : ovule ratio was estimated in the same way for the two planted populations of *C. caesius* in the Sepilok Arboretum and Kolapis A respectively.

Results

Insect pollination

The visitors to the flowers of both species of rattan are summarised in Tables 2(i), 2(ii), 3(i) and 3(ii). In *C. subinermis*, the most abundant diurnal visitors were the sweat bees, notably *Trigona laeviceps*, *T. melina* and *T. apicalis*, honey bees (*Apis cerana*, Fig. 1) and ants (Formicidae); and the most abundant nocturnal visitors were moths of the families Pyralidae and Noctuidae. In *C. caesius*, the most common visitors were also the diurnal sweat and honey bees and the nocturnal pyralid and noctuid moths (Fig. 2). The temporal variations in the number of the two main groups of visitors, moths and trigonid bees, are exemplified by those which visited the inflorescences of *C. subinermis* on Berhala Island illustrated in Fig. 3 and 4 which show clearly that the trigonid bees were active diurnally, and the moths were active at night. The abundance of the different groups of visitors is exemplified by those visiting *C. subinermis* as shown in Fig. 5 and 6. The pollen loads on the body of some of the insect visitors sampled during observations 1.3, 1.4, 2.4–2.7 are shown in Tables 4 and 5. Pollen was mostly found on the proboscis and legs of the moths, and the abdomen, legs, wings, thorax and corbicula (pollen baskets) of the bees. *Trigona* bees and moths, the most abundant groups of visitors, ants and other insects were also found visiting fallen fertile male and sterile male flowers. As observed on the insect visitors, the pollen grains are sticky and dispersed in clumps.

Wind pollination

Table 6 summarises the results of the study on the dispersal of pollen by wind. The maximum horizontal distance of dispersal was 4m, and the distance in different directions varied depending on the direction of the prevailing wind when most of the pollen grains were shed from dusk to about midnight. Assuming the density of pollen grains sampled from stem no. 2.1 on 6th January, 1994, at 1 m from the inflorescence was the average density from 0 to 1.5 m from the stem, and that at 2, 3 and 4 m was the average density from 1.5 to 2.5, 2.5 to 3.5 and 3.5 to 4.5 m respectively, the distribution of pollen dispersed was calculated and is given in Table 7. It is estimated that 88% of the pollen was dispersed within 3.5m from the inflorescence.

Pollen grains in male flowers and pollen : ovule ratio

The number of pollen grains in the male flowers of *C. subinermis* prior to anthesis was estimated to be 74,000 (S.D. = 14,000) per flower, and that in the fallen flower 12,000

Table 2(i) Visitors to female flowers of *Calamus subinermis*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9) , D = Very rare (<3). n.i. = not identified. The most abundant visitors are the trigonids, ants and moths.

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Coleoptera	Anthicidae	? *Formicomus* sp.	D	D
	Cerambycidae	*Sybra* cf. *binotata* Gahan	D	D
	Chrysomelidae	? *Taumacera* sp.	D	D
Elateridae	Elateridae	*Chiagosnius* sp.	D	D
		Ganoxanthus sp.	D	D
	Scarabaeidae	*Dichelomorpha* sp.	D	D
	Seirtidae	*Seirtes uniformis* Waterhouse	D	D
	Scolytidae	*Coccotrypes gedeanus* (Eggers)	D	D
	Tenebrionidae	*Plamius* sp.	D	D
	Curculionidae	n.i.	D	D
Collembola	Etomobryidae	? *Lepidocyrtus* sp.	D	D
Dictyoptera	Blattidae	*Periplaneta* sp.	D	N
Diptera	Asilidae	? *Leptogaster* sp.	D	D
	Calliphoridae	*Hemipyrellia ligurriens* (Wiedemann)	D	D
	Chloropidae	n.i.	D	D
	Culicidae	n.i.	D	D
	Drosophilidae	*Microdrosophila* sp.	C	D
		n.i.	C	D
	Platystomatidae	*Scholastes* sp.	D	D
	Sarcophagidae	*Sarcophaga* / *Parasarcophaga* sp.	D	D
	Sciaridae	n.i.	D	D
	Syrphidae	*Dideopsis aegrota* (Fabricius)	D	D
	Tachinidae	n.i.	D	D
	? Tipulidae	n.i.	D	D

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(Table 2(i) continued)

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Hymenoptera	Apidae	*Apis cerana* Fabricius	B	D
		Trigona apicalis Smith	A	D
		Trigona atripes Smith	A	D
		Trigona geissleri Cockerell	A	D
		Trigona melina Gribodo	A	D
		Trigona laeviceps Smith	A	D
	Halictidae	*Lasioglossum* sp.	D	D
	Ichneumonidae	*Apophua* sp.	D	D
		Pristomerus sp.	D	D
	Scelionidae	Scelioninae, n.i.	D	D
	Vespidae	*Parischnogaster* sp.	D	D
		Rhynchium sp.	D	D
		Paraleptomenes sp.	D	D
	Formicidae	*Camponotus* sp.	B	N
		Polyrhachis sp.	C	D/N
		Crematogaster sp.	A	D/N
		Formicine ants	A	D/N
Hemiptera	Plataspidae	*Brachyplatys subaeneus* Westwood	D	D
Lepidoptera	Blastobasidae	n.i.	D	D
	Cosmopterigidae	*Labdia oxychlora* Meyrick	D	D
	Gelechiidae	*Hypatima* sp.	D	D
	Pyralidae	*Lamprosema* sp.	B	N
		Psara playcapna (Meyrick)	B	N
		Ravanoa xiphialis Walker	B	N
		Sufetula sunidesalis Walker	B	N
		Tabidia sp.	B	N
		n.i. (2 species)	D	N
		Badiza ereboides Walker	C	N
		Micreremites sp.	B	N
	Noctuidae	*Naarda ? ineffectalis* Walker	B	N
		Nola sp.	C	N
		Progonia oileusalis Walker	D	N
		n.i. (2 species)	D	N
	Arctiidae	*Trischalis subaurana* Walker	D	N
	Thyrididae	*Pharambara splendida* Butler	D	N
Orthoptera	Gryllidae	n.i. (Cricket)	D	N
	Acrididae	n.i. (Small grasshopper)	D	D/N

Table 2(ii) Visitors to male flowers of *Calamus subinermis*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9), D = Very rare (<3). n.i. = not identified.

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Araneida	Araneidae	n.i. (Spider)	D	N/D
Coleoptera	Curculionidae	n.i.	B	N
Dermaptera	n.i.	n.i.	D	N
Diptera	Culicidae	n.i. (3 species)	C	D/N
	Tabanidae	*Tabanus* sp.	C	D
	Sarcophagidae	*Sarcophaga* sp.	C	D
Hemiptera	Coccidae	n.i.	C	D/N
Hymenoptera	Apidae	*Apis cerana* Fabricius	B	D
		Trigona laeviceps Smith	A	D
		Trigona melina Gribodo	A	D
		Trigona apicalis Smith	A	D
	Vespidae	*Vespa affinis* Linnaeus	C	N
	Eumenidae	*Eumenes* sp.	C	D
	Formicidae	*Camponotus* sp.	A	D/N
		Polyrhachis sp.	C	D/N
		Crematogaster sp.	A	D/N
		Formicine ants	A	D/N
Lepidoptera	Pyralidae	*Pycnarmon* sp.	B	N
		Herculia sp.	B	N
		Nacoleia sp.	A	N
		Pleuroptya sp.	A	N
		Psara playcapna (Meyrick)	B	N
		Tabidia sp.	C	N
		Lamprosema sp.	B	N
		n.i. (8 species)	A/B	N
	Geometridae	n.i. (2 species)	A	N

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(Table 2(ii) continued)

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Lepidoptera	Noctuidae	*Nola* sp.	B	N
		n.i. (5 species)	B	N
Neuroptera	n.i.	n.i	D	N
Orthoptera	Gryllidae	*Gryllacris* sp.	D	N
Squamata	Gekkonidae	n.i. (Lizard)	D	N

Table 3(i) Visitors to female flowers of *Calamus caesius*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9) , D = Very rare (<3). n.i. = not identified.

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Anura	n.i	n.i. (Frog)	D	N
Araneida	Araneidae	n.i. (Spider)	D	N/D
Chiroptera	n.i.	n.i. (Bat)	D	N
Coleoptera	n.i.	n.i. (4 species)	D	N
Dictyoptera	Blattidae	*Periplaneta* sp.	D	N
Diptera	Culicidae	n.i. (2 species)	C	D/N
Hymenoptera	Apidae	*Apis cerana* Fabricius	B	D
		Trigona itama Cockerell	C	D

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(Table 3(i) continued)

Order	Family	Species	Abundance	Diurnal (D)/ Nocturnal (N)
Hymenoptera		*Trigona melina* Gribodo	B	D
		Trigona laeviceps Smith	A	D
		Trigona melanocephala Gribodo	B	D
		n.i.	C	N
	Eumenidae	*Eumenes* sp.	D	D
	Formicidae	*Camponotus gigas* Latr.	D	N
	Ichneumonidae	n.i. (2 species)	D	D
	Stephanidae	n.i.	D	D
Lepidoptera	Pyralidae	*Circobotys* sp.	B	N
		Nomis sp.	A	N
		n.i. (3 species)	A	N
	Noctuidae	*Thalathoides* sp.	B	N
		Nola sp.	B	N
		n.i. (2 species)	B	N
	Arctiidae	n.i. (2 species)	B	N
Orthoptera	Gryllidae	n.i. (Cricket)	D	N

(S.D. = 4,000) per flower. In *C. caesius* the corresponding number of pollen grains was estimated to be 76,000 (S.D = 15,000) and 13,000 (S.D. = 4,000) respectively. The fallen flowers thus contained 16–17 % of the original number of pollen grains before anthesis.

The pollen : ovule ratio was estimated to be 93,000 in *C. subinermis* in the natural population on Berhala Island, and 360,000 and 420,000 (average: 390,000) in the planted populations of *C. caesius* in the Sepilok Arboretum and Kolapis A respectively (Table 8).

Table 3(ii) Visitors to male flowers of *Calamus caesius*. Abundance (Number of individuals observed per day on a typical stem with about 2,000 male flowers or about 400 dyads in bloom) : A = Very abundant (>30), B = Moderately abundant (10–30), C = Rare (3–9) , D = Very rare (<3) n.i. = not identified.

Order	Family	Species	Abundance	Diurnal (D) / Nocturnal (N)
Araneida	Araneidae	n.i. (Spider)	D	N/D
Coleoptera	Curculionidae	n.i.	B	N
	Cantharidae	*Rhagonycha* sp.	D	D
	Chrysomelidae	n.i.	D	D
Dermaptera	n.i.	n.i.	D	N
Dictyoptera	Blattidae	*Periplaneta* sp.	D	N
Diptera	Culicidae	n.i.	C	D/N
	Tabanidae	*Tabanus* sp.	C	D
	Sarcophagidae	*Sarcophaga* sp.	C	D
	Tephritidae	*Dacus* sp.	C	D
Hemiptera	Miridae	*Lygus* sp.	D	D
	Reduviidae	n.i.	D	D
Hymenoptera	Apidae	*Apis cerana* Fabricius	B	D
		Trigona melina Gribodo	C	D
		*Trigona laevicepss*Smith	A	D
		Trigona melanocephala Gribodo	B	D
		n.i.	C	D
	Pompilidae	*Ammophila* sp.	D	D
	Vespidae	*Eumenes* sp.	C	D
	Formicidae	*Pheidole* sp.	A	D/N
	Ichneumonidae	n.i. (2 species)	D	D
Lepidoptera	Pyralidae	*Circobotys* sp.	A	N
		Nomis sp.	B	N
		Glyphodes stolalis Guenee	B	N
		Herpetogramma sp.	C	N
		Pronomis sp.	A	N
	Noctuidae	*Thalathoides* sp.	B	N
		n.i. (3 species)	B	N

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(Table 3(ii) continued

Order	Family	Species	Abundance	Diurnal (D) / Nocturnal (N)
Lepidoptera	Geometridae	*Callopistria* sp.	A	N
		Ornithospila submonstrans Walker	A	N
Orthoptera	Gryllidae	*Gryllus* sp.	D	N

Table 4 Pollen load on some insect visitors to flowers of *Calamus subinermis*. Pollen Load: A = High (more than 20 pollen grains per mm^2), B = Medium (5–20 pollen grains per mm^2) C = Low (1–4 pollen grains per mm^2), D = None. Only *C. subinermis* pollen grains were counted.

No.	Visitor	Pollen load	Parts of body on which pollen grains were observed
1.	*Pycnarmon* sp. (Pyralidae)No.	C	Proboscis, legs
2.	*Herculia* sp. (Pyralidae)	D	–
3.	*Nacoleia* sp. (Pyralidae)	D	–
4.	*Pleuroptya* sp. (Pyralidae)	A	Proboscis
5.	Geometridae (Moth)	D	–
6.	Noctuidae (Moth)	D	–
7.	Noctuidae (Moth)	B	Proboscis
8.	*Trigona laeviceps*	A	Abdomen, legs, wings, corbicula
9.	*Trigona melanocephala*	A	Abdomen, legs, thorax, wings, corbicula
10.	*Trigona itama*	C	Abdomen, legs, wings, corbicula
11.	*Trigona melanocephala*	B	Legs, corbicula
12.	*Trigona laeviceps*	D	–

Fig. 1. A bee (*Apis cerana*) visiting male flowers of *Calamus subinermis* in Berhala Island. Most of the flowers on the rachillae have abscissed by dawn.

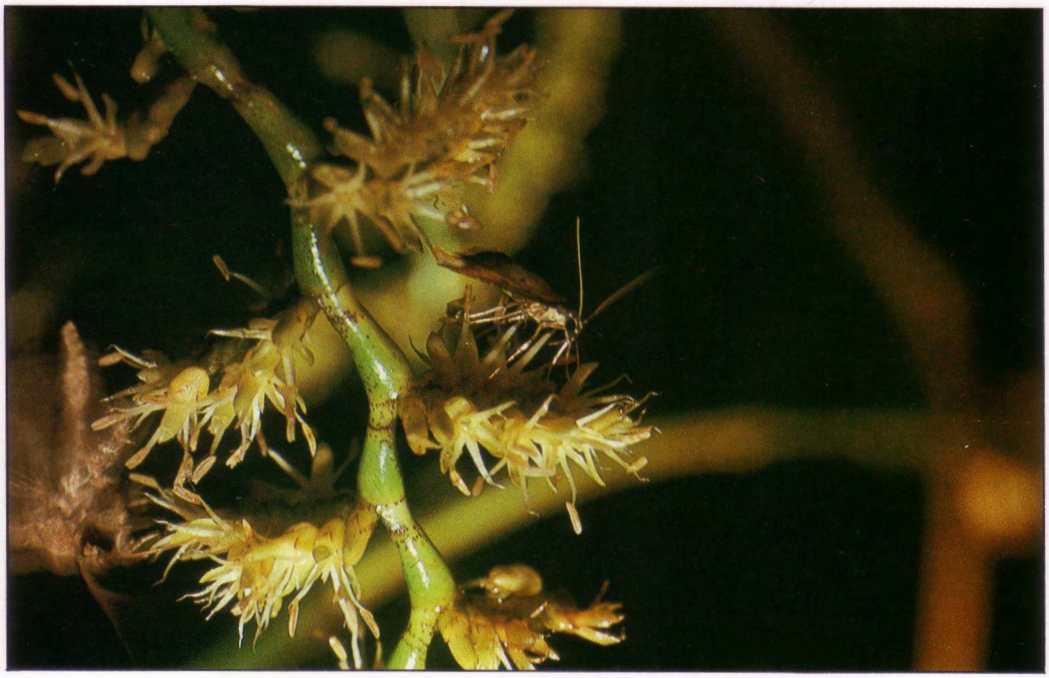
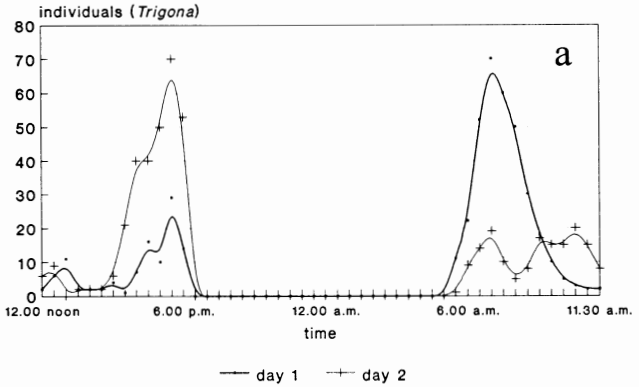


Fig. 2. Moths visiting a male inflorescence of *Calamus caesius* in Kolapis A.



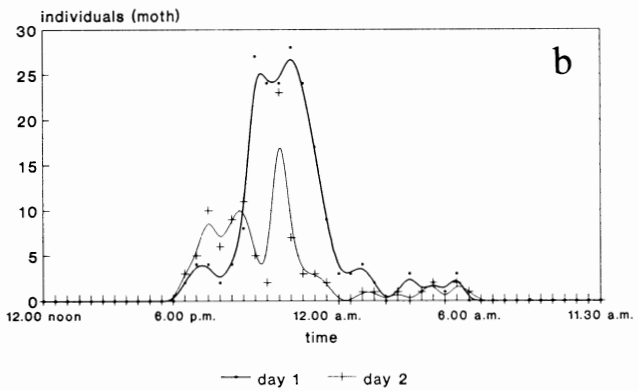
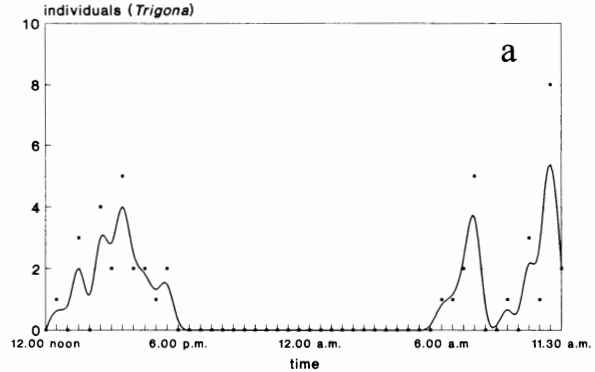


Fig. 3. Number of trigonids (a) and moths (b) visiting a male inflorescence of *Calamus subinermis* on two consecutive days on Berhala Island in September, 1993.



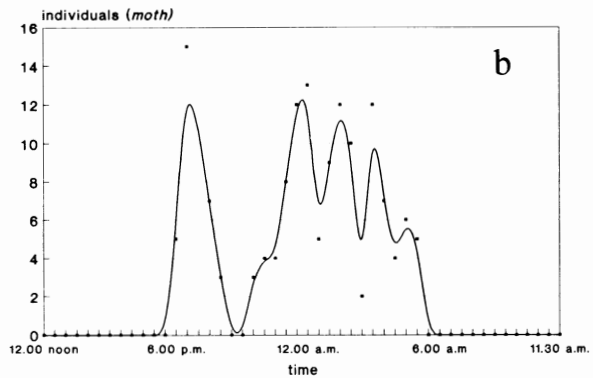


Fig. 4. Number of trigonids (a) and moths (b) visiting a female inflorescence of *Calamus subinermis* on Berhala Island in one day in September, 1993.

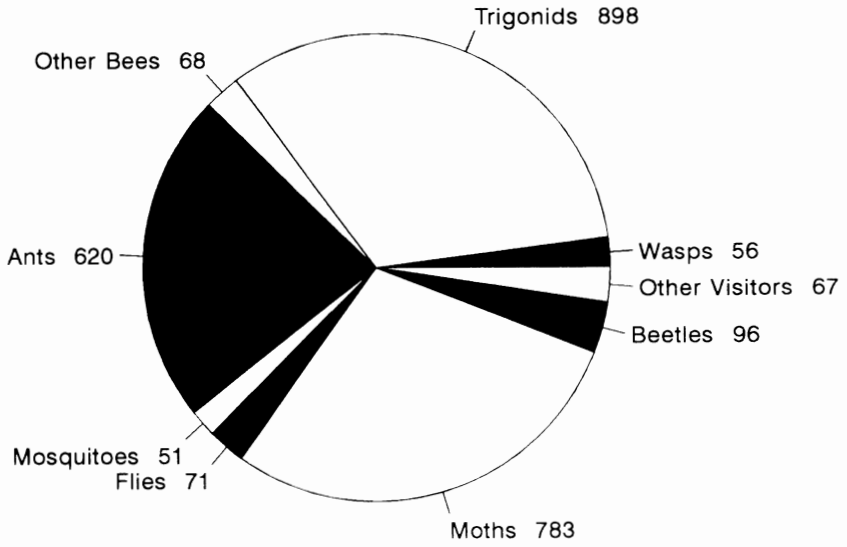


Fig. 5. Abundance of different groups of insect visitors to a male inflorescence of *Calamus subinermis* on Berhala Island in two days in September, 1993. Numbers following the names of the insect groups are those recorded.

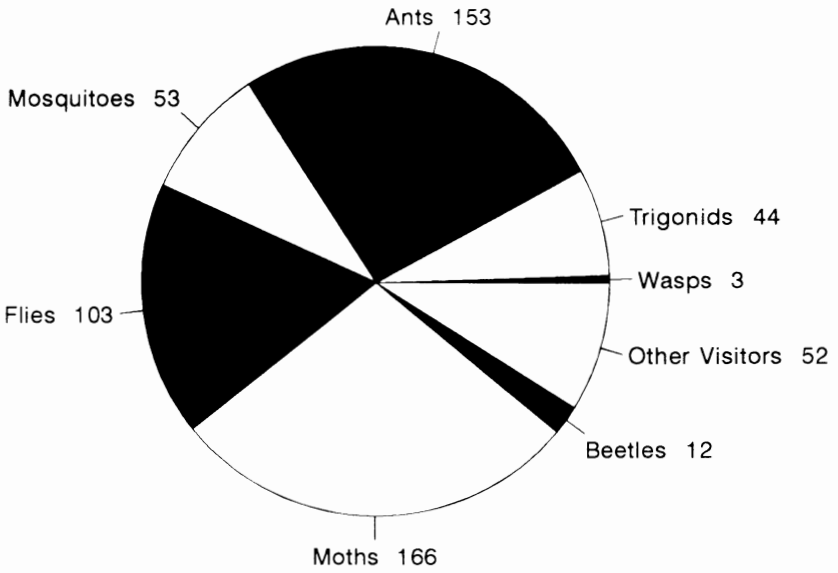


Fig. 6. Abundance of different groups of insect visitors to a female inflorescence of *Calamus subinermis* on Berhala Island in one day in September, 1993. Numbers following the names of the insect groups are those recorded.